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Sequences, stratigraphy and scenarios: what can we say about the fossil record of the earliest tetrapods?

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Past research on the emergence of digit-bearing tetrapods has led to the widely accepted premise that this important evolutionary event occurred during the Late Devonian. The discovery of convincing digit-bearing tetrapod trackways of early Middle Devonian age in Poland has upset this orthodoxy, indicating that current scenarios which link the timing of the origin of digitated tetrapods to specific events in Earth history are likely to be in error. Inspired by this find, we examine the fossil record of early digit-bearing tetrapods and their closest fish-like relatives from a statistical standpoint. We find that the Polish trackways force a substantial reconsideration of the nature of the early tetrapod record when only body fossils are considered. However, the effect is less drastic (and often not statistically significant) when other reliably dated trackways that were previously considered anachronistic are taken into account. Using two approaches, we find that 95 per cent credible and confidence intervals for the origin of digit-bearing tetrapods extend into the Early Devonian and beyond, spanning late Emsian to mid Ludlow. For biologically realistic diversity models, estimated genus-level preservation rates for Devonian digitated tetrapods and their relatives range from 0.025 to 0.073 per lineage-million years, an order of magnitude lower than species-level rates for groups typically considered to have dense records. Available fossils of early digitated tetrapods and their immediate relatives are adequate for documenting large-scale patterns of character acquisition associated with the origin of terrestriality, but low preservation rates coupled with clear geographical and stratigraphic sampling biases caution against building scenarios for the origin of digits and terrestrialization tied to the provenance of particular specimens or faunas.

Keywords: birth–death models; Devonian; fossil record bias; origin of tetrapods; palaeobiology; preservation rate

1. INTRODUCTION

Temporal estimates for the origin of digit-bearing tetrapods have been calibrated overwhelmingly by the stratigraphic distribution of skeletal remains (e.g. [1–4]). By contrast, putative trace fossils of digitated track-makers have been sidelined from debate [5], even though some trackways substantially predate the earliest body fossils for which digit-bearing limbs are known [6,7]. Interest in ichnofossil data as an important line of evidence in documenting the emergence of digit-bearing limbs has been rekindled by the report of tetrapod trackways from Zachelmie, Poland, dated to the early Middle Devonian (Eifelian, *ca* 395 Ma; [8]). This discovery upsets the orthodox view that digit-bearing tetrapods originated in the Late Devonian [1–4].

Less clear, however, are the implications of these trackways for the overall quality of the fossil record of early tetrapods. Skeletal remains of digitated Devonian forms and their closest relatives have always been exceedingly rare. Although limited in number and completeness, these fossils have delivered a detailed picture of the

sequence of anatomical changes associated with the emergence of digitated tetrapods from their fish-like ancestors. Discoveries continue to add detail and, while some character incongruence certainly exists (see cladistic ‘experiments’ in Callier *et al.* [9]), these finds do not generally alter a consistent phylogenetic backbone defined by taxa known from reasonably complete material. Instead, new fossils often slot into a pre-existing framework of relationships and character transformation [10].

The ever more detailed picture of the sequence of major morphological shifts associated with the origin of digit-bearing tetrapods contributes to the illusion of a complete record. This highlights a dichotomy in the way the quality of palaeontological archives might be perceived: the adequacy of available material for reconstructing relationships and patterns of character transformation, versus the rate at which lineages are preserved, recovered and reported. The Zachelmie trackways do not challenge existing cladistic topologies or inferred sequences of morphological change, but they do invite investigation into the sampling quality of the skeletal record of digitated tetrapods and their close relatives, and the ability of this archive to provide absolute dates for important events in early tetrapod evolution.

Here, we address a series of broadly framed questions raised by the discovery of the Zachelmie footprints. First,

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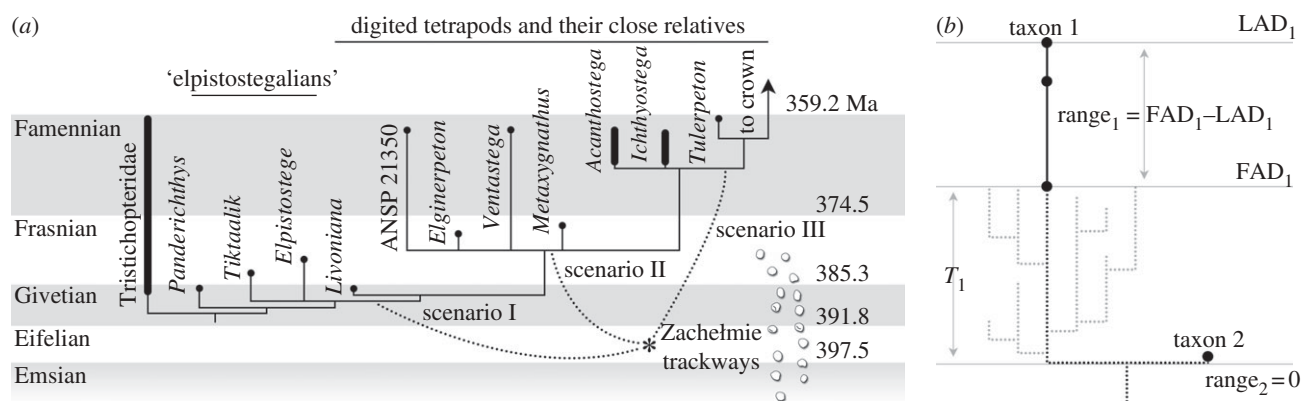


Figure 1. (a) Phylogeny of Devonian digit-bearing tetrapods and their immediate fish-like relatives calibrated based on the distribution of skeletal remains alone [8]. The Eifelian Zachemie trackways predate the earliest body fossils known for any of these groups. We examine three possible phylogenetic placements for the trackmaker, labelled as scenarios I–III. (b) Stratigraphic data bearing on estimates of preservation rate. The distribution of observed taxonomic durations, the difference between first and last appearance dates (FAD and LAD) for individual taxa, is a function of extinction and preservation rates. Ghost lineages are stratigraphic gaps implied by phylogeny (black dotted lines), and indicate the minimum waiting time T_1 for the first member of a given clade to enter the fossil record. More realistic waiting times can be inferred by using models of cladogenesis to estimate the cumulative duration of branches collateral to the ghost lineage that have likewise gone unsampled (grey dotted lines).

how good is the body fossil record of Devonian digit-bearing tetrapods and their nearest fish-like relatives, measured quantitatively as preservation rate? Second, what is the effect of the Zachemie trackways on estimates of preservation rate among digit-bearing tetrapods and their nearest relatives, and how surprising is the age of these footprints given our previous understanding of the fossil record? Third, given new insights about the nature of the record informed by the Polish footprints, what can be said about the probable timing of the origin of digits?

2. MATERIAL AND METHODS

(a) *Stratigraphic conventions*

To facilitate the estimation of stratigraphic ranges and first appearances, we divided relevant stages of the Devonian and Silurian into smaller units of more comparable duration. Details of our stratigraphic binning scheme, along with ranges for individual taxa, are given in the electronic supplementary material.

(b) *Nomenclature and phylogenetic framework*

In this paper, we adopt the total-group nomenclature for Tetrapoda [4], and refer to those members of the clade which exhibit digits as digit-bearing tetrapods. We apply ‘elpistostegalian’ in its traditional capacity: a term encompassing a grade of stem tetrapods including taxa like *Panderichthys* and *Tiktaalik* but excluding digit-bearing tetrapods (contra [11]). ‘Osteolepiforms’ are members of the tetrapod total group outside ‘elpistostegalians’ plus digit-bearing forms.

The implications of the Zachemie trackways for the nature of the early tetrapod record hinge upon the phylogenetic placement of the trackmaker. According to the topology presented by Niedźwiedzki *et al.* [8], digit-bearing limbs minimally diagnose the clade comprising *Acanthostega* plus all more crownward taxa, and maximally diagnose the clade containing all taxa crownward of *Tiktaalik*. Niedźwiedzki *et al.* [8] place the trackmaker in an unresolved polytomy with *Acanthostega*, *Ichthyostega* and *Tulerpeton* plus the crown, but the trackmaker could branch from any point

crownward of *Tiktaalik*. As a reflection of uncertainty, we have explored three different scenarios that together span the range of probable phylogenetic solutions (figure 1a). These posit increasingly crownward positions for the trackmaker, which demand progressively longer stratigraphic gaps. We consider scenarios where the trackmaker branches: immediately crownward of *Tiktaalik* (scenario I); just outside the clade definitively diagnosed by digit-bearing limbs (scenario II); in the position proposed by Niedźwiedzki *et al.* [8] (scenario III).

Below, we discuss two phylogenetically explicit methods used to assess the impact of the Zachemie footprints upon our perception of the early tetrapod record. Details relevant to each approach appear in the next two sections and the electronic supplementary material. All analyses were performed using scripts written in R [12].

(c) *Bayesian credible intervals on clade origins*

The phylogenetic scenarios discussed above constrain minimum dates of origin for the clade comprising the Zachemie trackmaker plus all more crownward taxa. In order to test whether these new age estimates are inconsistent with our previous understanding of divergence times, we have generated credible intervals for the nodes in the cladogram corresponding to the branching points of the trackmaker under scenarios I–III. We employ the method outlined in Hedman [13], which is based on the stratigraphic distribution of sequential outgroups to a focal clade. This approach requires that the appearance of successive outgroups in the fossil record corresponds to their branching order in a tree, but few empirical examples show perfect congruence between phylogeny and stratigraphy. We adopt a conservative solution to this problem (cf. [13], p. 24), and consider only those successive outgroups that appear in stratigraphic order. Details of our outgroup sequences are provided in the electronic supplementary material. Using this technique, we test whether the age of the Zachemie footprints fall beyond the lower 95 per cent credible interval for the origin of the most restrictive clade comprising the trackmaker plus the crown under scenarios I–III.

(d) *Measuring preservation rates and maximum-likelihood confidence intervals*

The completeness of the fossil record involves the interplay of extinction rate (q), which determines the duration of individual taxa, and preservation rate (r), which indicates how likely a taxon is to enter the fossil record as a function of its longevity. We take ‘preservation rate’ to include the complex set of processes that result in the appearance of a fossil in a database, including fossilization, discovery, identification and description. Our approach to estimating the quality of the early record of digit-bearing tetrapods and their closest relatives draws upon two kinds of data with theoretical relationships to these parameters [14,15]: (i) the distribution of observed stratigraphic ranges of individual taxa, and (ii) the duration of stratigraphic gaps between the evolutionary origin of taxa and their first appearance in the fossil record (figure 1b and discussion in the electronic supplementary material). For these analyses, we limit our consideration to a subset of early tetrapods: tristichopterids plus all more crownward Devonian taxa [16–19]. The anatomy and systematics of these groups have been thoroughly revised by a consistent set of researchers over the past two decades, resulting in a standardized taxonomy combined with a robust phylogenetic framework. By contrast, the taxonomy of most ‘osteolepiforms’ (exclusive of tristichopterids) is in a comparative state of disarray. Many of the genera thought to branch from this part of the tetrapod tree appear to represent poorly characterized ‘wastebin’ taxa. All of our analyses were conducted at the genus level.

The first kind of data, taxonomic range-frequency distributions, can be gathered independently of a phylogenetic backbone. Here, we employ the continuous-time, maximum-likelihood approach for estimating q and r outlined by Foote [15], and refer readers to that paper and our electronic supplementary material for details. Our database comprises those genera shown to branch within the clade consisting of tristichopterids plus digitated tetrapods or taxa that have been associated with this radiation. We have adopted two methods for estimating taxonomic durations. Both approaches consider those taxa occurring at a single horizon (i.e. a single fossil or several fossils within a single formation or formations that are lateral equivalents) to have a stratigraphic range of 0 Ma. These methods differ in their treatment of multi-horizon taxa (i.e. those occurring in two or more formations that are not lateral equivalents). The first approach (‘whole’) assigns these taxa an age equivalent to the summed duration of sub-stages, or the duration of the single interval if the taxon occurs in stratigraphically successive formations within a single substage. The second approach (‘fractional’) assigns the same taxa an age equivalent to half the duration of the sub-stages of first and last appearance, plus the full duration of all intervening intervals. Single-substage, multi-horizon taxa are assigned a duration equal to half that of the interval in which they appear. We also adopt two contrasting treatments of fossils whose taxonomic identifications are equivocal. The first approach granted each indeterminate fossil status as a distinct genus (dataset A), while the second excluded such materials entirely (dataset B). These end-member approaches to taxonomy and stratigraphy aim to deliver a range of estimated preservation rates that reflect uncertainty.

We derived the second class of data, stratigraphic gaps (ghost lineages *sensu* [20]), from a hypothesis of phylogeny [8]. Our analysis seeks those values of q and r that maximize the likelihood of observing these gaps and the genus ranges in our

database (electronic supplementary material). A ghost lineage represents the minimum estimate of the waiting time (in lineage-million years; LMa) from the evolutionary origin of a group to its first appearance in the fossil record (first appearance date (FAD); figure 1b). There is considerable uncertainty surrounding the true duration of waiting times, leading us to explore multiple models that differ in how they estimate the waiting times implied by ghost lineages. All approaches use minimum estimates of ghost lineage duration, with no accommodations made for clades issuing from the backbone of tetrapod phylogeny that fail to enter the fossil record. These conventions bias our analyses towards recovering higher preservation rates, and thus provide a conservative test of the assertion that the early tetrapod record is well sampled.

The first model (‘literal’) posits no collateral branches issuing from ghost lineages. Consequently, the magnitude of any given waiting time is equal to that of its associated ghost lineage T , and can be measured directly. The second model (‘conditional BD’) integrates birth–death models of cladogenesis [21] to estimate the cumulative duration of the ghost lineage plus unsampled, collateral branches accumulated before the FAD of the focal group [22]. Estimated waiting time for a given clade is a function of four parameters under this approach. The first two are measured directly: ghost lineage duration T and the number of taxa N (both sampled and implied by phylogeny) whose appearance together mark the clade’s FAD. The third parameter is extinction rate q , and it must be estimated. We have adopted two approaches to modelling the final parameter, origination rate p . Our first approach (‘conditional BD₁’), matches that applied by Foote *et al.* [22]. This variant constrains net growth rate by estimating p as a function of q , N and T . Our second approach (‘conditional BD₂’) builds upon the observation of depressed rates of origination relative to extinction during the Middle–Late Devonian (e.g. [23]), and estimates p as one half of q . In these BD models, our estimate of waiting time is conditioned on the survival of at least N lineages to T for each ghost lineage. These approaches—literal, BD₁ and BD₂—deliver a range of diversity profiles (electronic supplementary material) that accommodate uncertainty surrounding true waiting times.

The likelihood function for q and r given taxonomic ranges and our sample of ghost lineages is given in the electronic supplementary material. We maximized this expression numerically. Because our approach explicitly considers a set of gaps implied by phylogeny, it allows us to compare our inferences about the nature of the early tetrapod fossil record before and after the discovery of the Zachelmie trackways. Specifically, we examined whether estimates of q and r made using the distribution of gaps implied by the Polish footprints differ significantly from those estimated from the distribution of gaps inferred prior to the discovery of these trackways using likelihood-ratio tests (LRT). The likelihood ratio (LR) is given by the formula:

$$LR = -2 \ln \left(\frac{\ell(H_0)}{\ell(H_1)} \right)$$

where both likelihoods are calculated using the dataset that excludes the Zachelmie trackways; $\ell(H_1)$ is the maximum-likelihood solution for that dataset, and $\ell(H_0)$ is the likelihood of the (constrained) parameter pair estimated based on the stratigraphic implications of the Polish footprints. In this case, the LR approximates a χ^2 -distribution with two degrees of freedom.

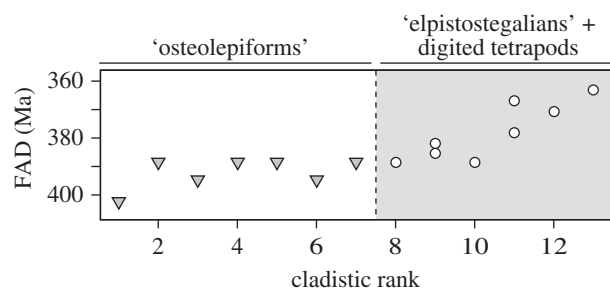


Figure 2. Congruence between the order of first appearance date (FAD) of Devonian branches along the tetrapod stem and their cladistic ranks (node height; increasing rank indicates increasing proximity to the crown node). Node ranks based on a composite topology (digitated tetrapods and ‘elpistostegalian’: [8]; ‘osteolepiforms’: [17,19]). When all taxa are considered, FAD and cladistic rank are strongly correlated with high degrees of statistical significance (Spearman rank-order correlation; $\rho = -0.90$, $p = 4.8 \times 10^{-7}$). There is excellent congruence between stratigraphy and phylogeny for ‘elpistostegalian’ and digitated tetrapods ($\rho = -0.83$, $p = 0.0017$; cf. [8]), but not when ‘osteolepiforms’ are considered in isolation ($\rho = -0.42$, $p = 0.35$). Similar results are obtained when alternative topologies are used for the ‘osteolepiform’ segment of the stem (electronic supplementary material).

We have also applied this likelihood approach to provide confidence limits on the timing of the origin of digit-bearing limbs in light of the Zachelmie trackways. Specifically, we asked how ancient digit-bearing tetrapods could be before we reject parameter estimates made with reference to the Polish footprints at the $\alpha = 0.05$ level. This date represents the 95 per cent confidence limit for the emergence of digitated tetrapods given present understanding of the record. We have accomplished this iteratively, by (i) calculating the likelihood of the parameter pair estimated from data including the Zachelmie trackways, but which place the origin of digitated tetrapods at some time greater than 395 Ma, (ii) calculating the LR and corresponding p -value, and (iii) repeating this procedure until p reaches the desired value. Since we do not know the precise phylogenetic position for the origin of digits, we completed this procedure under each of the placements (I–III) discussed above. Results reviewed below appear in full in the electronic supplementary material.

3. RESULTS

(a) Correspondence between phylogeny and stratigraphy

When only skeletal remains are considered, there is a strong correlation between the node rank and the FAD for successive branches along the tetrapod stem (figure 2). This significant relationship is robust to contrasting phylogenetic interpretations (Spearman rank-order correlation: $\rho = -0.90$, $p = 4.8 \times 10^{-7}$; electronic supplementary material). Although there is excellent congruence between stratigraphy and phylogeny when the stem is considered as a whole, this relationship does not hold for ‘osteolepiforms’ in isolation. In contrast to digitated tetrapods plus ‘elpistostegalian’, whose FADs closely match the predictions of branching order (Spearman rank-order correlation: $\rho = -0.83$, $p = 0.0017$), there is no clear relationship between phylogeny and stratigraphy for ‘osteolepiforms’ (Spearman

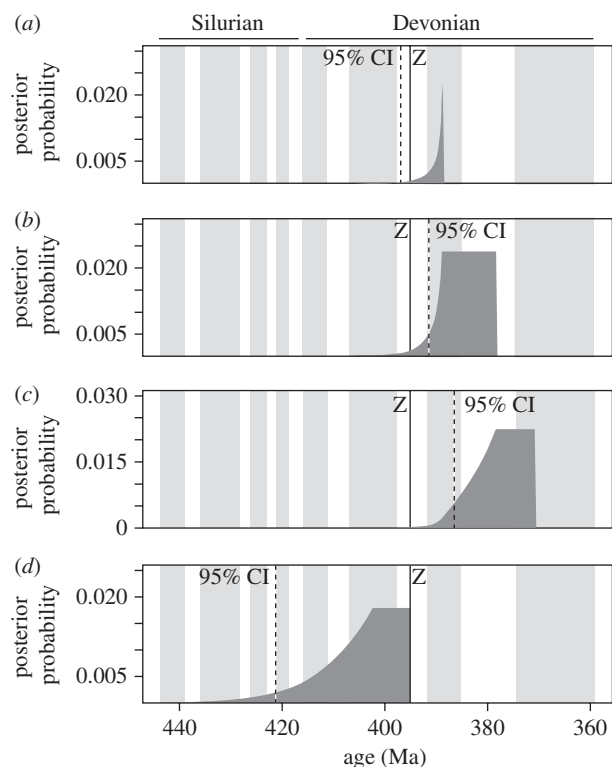


Figure 3. Posterior probability distributions for the date of origin for digitated tetrapods. In all plots, the solid vertical line indicates the age of the Zachelmie trackways (395 Ma; Z), while the dashed line indicates a lower 95% credible interval (one-tailed) for the first appearance of the clade of interest (95% CI). Alternating grey and white fields indicate stage-level divisions of the Silurian and Devonian. The first three panels do not consider the Polish footprints, and give credible intervals for the FAD of the most restrictive clade containing the trackmaker and the tetrapod crown under scenarios I–III discussed in the text and in figure 1. For each, the p -value indicates the posterior probability of digitated tetrapod origin at 395 Ma or earlier. (a) Scenario I ($p = 0.077$). (b) Scenario II ($p = 0.013$). (c) Scenario III (preferred placement of Niedźwiedzki *et al.* [8]; $p = 0.0015$). (d) Posterior probability distribution for the origin of digitated tetrapods, based on the age of the Zachelmie trackways and successive, stratigraphically consistent outgroups. The lower 95% credible interval for the origin of digitated tetrapods lies at 421.3 Ma (Gorstian–Ludfordian boundary); estimated origin is 403.6 Ma (early Emsian). Two-tailed 95% credible interval about this estimate (427.4–395.7 Myr ago) extends into the mid Silurian (Sheinwoodian).

rank-order correlation: $\rho = -0.42$, $p = 0.35$). Instead, most ‘osteolepiform’ clades that can be placed within a tree appear within a narrow window spanning the Eifelian–Givetian.

(b) Estimated credible intervals

Each hypothesized placement of the Zachelmie trackmaker corresponds to a different posterior probability distribution for the age of the relevant split estimated with reference to body fossil evidence. In the case of scenario I, the Polish trackways narrowly fall within the 95 per cent credible interval for the first appearance of the clade comprising *Livoniana* and all more crownward taxa ($p = 0.077$; figure 3a). Thus, if the trackmaker branches from the node most distal to the crown

permitted by our current anatomical understanding, the trackways do not represent a statistically significant departure from the body fossil record. This is not the case for scenarios II and III, both of which posit more crownward placements of the trackmaker. In each case, the age of the footprints falls outside the 95 per cent credible interval ($p = 0.013$ and 0.0015 , respectively; figure 3*b,c*). This result indicates that the age of these trackways is statistically inconsistent with our previous understanding of the stratigraphic distribution of early digit-bearing tetrapods and their fish-like relatives, forcing a substantial reconsideration of the nature of the Devonian tetrapod record.

(c) *Preservation rates and the quality of the early tetrapod record*

Depending on assumptions about stratigraphic ranges, cladogenic models and the status of indeterminate fossil material, we estimate values of r ranging from 0.044 to 0.18 per LMa^{-1} for Devonian digit-bearing tetrapods and their immediate outgroups when only the body fossil record is considered. Higher estimates of preservation rate derive from the less realistic literal diversity model that equates the magnitude of waiting time to any given FAD with the duration of its relevant ghost lineage. Estimates of r using the more realistic conditional BD diversity models (0.044 – 0.099 LMa^{-1}) agree quite closely with those made without reference to phylogeny, and which instead are based on stratigraphic range frequency distributions alone (0.042 – 0.085 LMa^{-1}).

The relevant question here is whether the preservation and extinction rates demanded by the Zachelmie trackways diverge significantly from those derived from body fossil data. Only with the stratigraphically most conservative phylogenetic placement of the trackmaker (scenario I), do the Polish footprints never force a significant change in q and r , and thus our estimates of the quality of the record of early digit-bearing tetrapods and their closest fish-like relatives (LRT; $p = 0.46$ – 0.90). Scenarios II (under both binning approaches for the BD_2 model, but only under the fractional binning scheme for the BD_1 and literal models) and III (under both binning approaches) do demand substantial shifts in parameter estimates relative to those made based on the skeletal record alone (LRT; $p = 0.00085$ – 0.043), with r as low as 0.025 LMa^{-1} for the BD_1 model. This value is approximately half that estimated from the body fossil record using the same model.

We also tested whether the Zachelmie trackways demand a significant reconsideration of the early tetrapod record if other putative traces of digitated forms that might have previously been considered anachronistic are taken at face value. We made estimates of q and r based on the body fossil record plus the Givetian–Frasnian Valentia Island footprints [6,7] under three alternative placements of their trackmaker (matching scenarios I–III). In most cases, there is no statistical difference between parameter estimates made with reference to these Irish trackways and those using temporal calibrations imposed by the Zachelmie footprints. Marginally significant shifts (LRT; $p = 0.035$ – 0.045) are confined to estimates made using the conditional BD_1 model under placements II and III, and are only found when stratigraphic ranges are tabulated according to the

fractional approach. For Hedman's [13] Bayesian method, the Zachelmie footprints fall within the 95 per cent credible interval when both trackmakers are placed according to scenario I ($p = 0.077$; distribution identical to that in figure 3*a*), but beyond it under scenarios II and III ($p = 0.018$; however, the Polish footprints do not remain a significant outlier if the true age of the Irish tracks exceeds their radiometric minimum age constraint by more than *ca* 3.5 Ma, see the electronic supplementary material). Thus, while the Zachelmie trackways predate the minimum age of the Valentia Island footprints, the former do not consistently demand reconsideration of the record of Devonian tetrapods when the latter are taken into account.

(d) *Timing the origin of digit-bearing tetrapods*

In the previous sections, we examined the degree to which the Zachelmie footprints force us to reconsider the fossil record of Devonian digit-bearing tetrapods and their relatives. This same framework allows us to ask an arguably more interesting question: given our knowledge of the Polish trackways and the body fossil record, what can we say about the probable timing of the origin of digitated limbs?

Using Hedman's [13] method, we estimate an origin for digitated tetrapods at 403.6 Ma (early Emsian), with a two-tailed 95 per cent credible interval of 427.4–395.7 Myr ago (Sheinwoodian–early Givetian). The 95 per cent credible interval (one-tailed) for first appearance is 421.3 Ma (Gorstian–Ludfordian boundary; figure 3*d*). We have also applied our maximum-likelihood approach to provide confidence limits on the origin of digit-bearing tetrapods. Depending on the phylogenetic placement of the trackmaker, stratigraphic binning scheme, taxonomic dataset and diversity model, this method delivers a 95 per cent lower bound ranging from a low of 398.9 Ma (late Emsian) to a high of 413.9 Ma (mid Lochkovian). Older dates derive from the more realistic conditional BD models, and we regard these as more reliable. Both sets of estimates are younger than those obtained from Hedman's [13] approach, but in no case can we reject the possibility of digitated tetrapods of Early Devonian age.

4. DISCUSSION

(a) *How good is the fossil record of early tetrapods?*

An obvious question is how our inferred preservation rates for Devonian digitated tetrapods and their close relatives compare with estimates made for other fossil groups. When stratigraphic ranges are considered in isolation ($r = 0.042$ – 0.085 LMa^{-1}), or when these data are combined with phylogenetically implied gaps plus biologically realistic models of diversification ($r = 0.025$ – 0.074 LMa^{-1}), we find genus-level preservation rates for early digit-bearing tetrapods and their immediate outgroups are comparable to those for Late Cretaceous mammal species (0.03 – 0.06 LMa^{-1} ; [22]) and mean values for a taxonomically diverse sample of invertebrate genera from the Palaeobiology Database [23]. Our rate estimates are roughly an order of magnitude lower than those for extremely well-sampled groups at the finest level of taxonomic resolution, like Cenozoic mammal species in North America (preservation probability = 0.25 per 0.7 Ma interval, $r = 0.41$ LMa^{-1}) or Jurassic bivalve species in Europe (preservation probability = 0.87 per 5 Ma interval, $r = 0.41$ LMa^{-1}) [14].

This is unsurprising. Before the Polish trackways highlighted the missing pre-Givetian record of ‘elpistostegians’ and digitated tetrapods, there were already indications of outstanding stratigraphic gaps in the Devonian tetrapod record. Most major piscine branches in tetrapod phylogeny (rhizodonts, osteolepidids *sensu stricto*, megalichthyids, canowindrids and tristichopterids) make their debut in the Eifelian–Givetian. Unlike more crownward stretches of the stem, where clade rank and FAD are tightly correlated, these deep branches show no clear relationship between stratigraphy and phylogeny (figure 2). This suggests three possibilities, which are not mutually exclusive: (i) a rapid diversification event, with short internodes separating successive branches; (ii) the failure of current cladograms to accurately capture true phylogenetic structure; and (iii) an exceedingly poor pre-Givetian record of stem tetrapods. Evidence that the final factor might play an important role comes from the Givetian Aztec Siltstone fauna of Antarctica [24,25], which yields some of the stratigraphically oldest representatives of several major stem tetrapod radiations. Despite their age, many of these taxa are not the most anatomically primitive members of their respective groups, but instead nest within clades bounded by younger taxa (*Aztecia* among rhizodonts and *Notorhizodon* among tristichopterids; [25,26]). Moving into the pre-Givetian record, there are many stem tetrapod fossils, but most are poorly documented or inadequately characterized. The oldest unambiguous stem tetrapods are from the late Emsian (*Kenichthys*; [17]), but the origin of the clade can be dated to no later than Lochkovian, as indicated by a diverse range of stem lungfishes from this stage (*Diabolepis*, *Youngolepis*, *Powichthys*). The only hints of stem tetrapods from this Early Devonian gap come in the form of undescribed remains from the Pragian of China [27].

There is a compelling relationship between stratigraphy and phylogeny for digit-bearing tetrapods and ‘elpistostegians’, leading to questions of how such a sequence could arise in the face of a highly incomplete record [8]. Given the small number of taxa concerned, it is possible that this pattern has arisen by chance alone, but we also note that stratophylogenetic fit is not inconsistent with low sampling rates. Just as extinction events are ‘smeared’ backwards in the fossil record (the Signor–Lipps effect; [28]), apparent originations are displaced forward relative to their true positions [29]. Furthermore, recovery rates for higher taxa are unlikely to be uniform over time, but more probably increase as diversity accumulates [30]. These two factors combine in such a way that we might expect the fossil record to preserve groups in an order approximating that dictated by phylogeny, even though these appearances are offset considerably from true times of origination.

(b) *Geographical bias in the record of Devonian digitated tetrapods and their relatives*

Knowledge of past biodiversity is dominated by the North American and European records [31], and the case is little different for Devonian stem tetrapods. Classic Euramerican deposits known to yield early digitated tetrapods and close relatives—including the Upper Old Red Sandstone of Scotland, the Catskill Formation of the USA, the Escuminac Formation of Canada and various strata of the Baltic states and Russia [32]—have been collected since the mid-late nineteenth century [33]. Many

important recent discoveries have come from Australia and Asia, but understanding of the record in these regions is still maturing. If only finds outside of Euramerica are considered, our compilation of digitated tetrapods and their closest ‘fish’ relatives is reduced to a meagre eight named genera, of which all are single-horizon taxa with the possible exception of *Eusthenodon* [26,34]. Estimates of preservation rate made from stratigraphic-range distributions derived exclusively from Euramerican fossil sites are higher than those from global data ($0.055\text{--}0.11\text{ LMa}^{-1}$ versus $0.042\text{--}0.085\text{ LMa}^{-1}$), and the contrast is more striking if only the European record is considered ($r = 0.094\text{--}0.18\text{ LMa}^{-1}$). We do not assert that fossilization rates are genuinely higher for Europe, but rather that they appear elevated owing to historically more extensive sampling there than in other regions.

Given that the present temporal picture of the emergence of digit-bearing tetrapods has been framed largely by European fossils, it is not unreasonable to suspect that surprising new finds might come from further afield; in comparison to the mature European record, those of Australia, Asia and, to a certain extent, North America (particularly the western part of the continent), are in their adolescence, with a patchy to virtually non-existent record in the rest of the world (Antarctica, [24]; Africa, [34]; South America, [35]). This conclusion assumes that the relative poverty of finds from outside Europe reflects differential sampling, rather than a highly provincialized palaeobiogeographical pattern.

(c) *Straigraphy, phylogeny and scenarios*

By demanding a much earlier origin for digits than previously believed, the Zachełmie footprints expose profound palaeontological gaps and highlight the need for a more circumspect view of the Devonian tetrapod record [8]. The unanticipated age and depositional environment of these trackways have prompted challenges to prevailing notions of early tetrapod evolution, but some new proposals rely on relatively direct readings of palaeontological archives, tied to either the observed stratigraphic distribution of taxa or the environmental association of specific specimens. We question whether such scenarios are appropriate in the face of what we now understand to be a very incomplete record.

First (Niedźwiedzki *et al.* [8], p. 47) present the Polish trackways as suggestive evidence that digitated tetrapods might have originated in littoral or intertidal environments, as opposed to the fluvial setting often proposed based on stratigraphically younger skeletal remains (for a summary, see [3]). We do not give preference to either of these specific hypotheses, and remain agnostic concerning the environmental locus for the appearance of digits. The Zachełmie tracks were made by a taxon of unclear phylogenetic position, and, despite their great age, we regard their implications for the environmental context of the emergence of digit-bearing tetrapods as similarly ambiguous. Skeletal remains of Devonian digitated tetrapods and their closest relatives derive from a diverse range of marine and continental facies ([32], table 1), and current uncertainties about the interrelationships and anatomy of some of these taxa means that the precise environmental context(s) for the origin of digits remains unclear. As a parallel example, we

point to the broad set of inferred habitats for some of the earliest cetaceans [36], and note that it is possible that important steps in the evolution of digits similarly occurred in a series of distinct settings.

Second, the Zachelmie tracks have inspired the notion that apomorphies common to digitated tetrapods and ‘elpistostegals’ might be convergent [37]. This hypothesis arises from the absence of any pre-Givetian skeletal remains attributed to the ‘elpistostegalian’ plus digitated tetrapod clade as it is presently understood, and proposes to fill this stratigraphic vacuum with ‘osteolepids’. The characters possessed by the Early-Middle Devonian members of this stem-tetrapod grade are such that if they are to bridge the temporal gap, exceptional parallelism must be invoked to explain the striking anatomical similarities between ‘elpistostegals’ and tetrapods. We question this stratophylogenetic scenario based on both the demonstrably spotty record of Devonian tetrapods and the robust support for the node uniting ‘elpistostegals’ and digitated tetrapods in cladistic analyses targeting the tetrapod stem [16,17,19] and those exploring osteichthyan interrelationships more generally [18,38].

The past two decades of research have demonstrated that character-based hypotheses of tetrapod evolution are very successful in predicting probable trait complexes in newly discovered taxa, regardless of their age. Now-iconic ‘missing links’ like *Tiktaalik*, greeted by much fanfare upon their arrival, did little to upset pre-existing hypotheses of large-scale character distribution and transformation [10]. The Zachelmie trackways and other seemingly anachronistic trace fossils shatter the notion that absolute timing of evolutionary events in early tetrapod evolution might be read more-or-less directly from stratigraphy. But the inadequacy of palaeontological data to address these temporal questions should not be confused with their capacity to tackle others. Imperfect as it is, the fossil record remains adequate to document what is arguably the key evolutionary element of the origin of digitated tetrapods: the sequence of morphological changes leading from aquatic vertebrates to terrestrial ones.

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